Evidence of concealment behavior by adult rainbow trout and brook trout in winter

Meyer KA, Gregory JS. Evidence of concealment behavior by adult rainbow trout and brook trout in winter.
Ecology of Freshwater Fish 2000: 9: 138–144. © Munksgaard, 2000

Abstract – There has been little investigation of the winter ecology of adult trout during winter, especially in regard to concealment behavior. We compared day *vs* night underwater counts of adult rainbow trout and brook trout from four streams. At water temperatures between 1°C and 9°C, daytime counts accounted for 44% and 16% of nighttime snorkeling counts for rainbow trout and brook trout adults, respectively. As winter progressed, nighttime counts declined more so for brook trout than rainbow trout, but the decline was not significant for either species. Nocturnalism of both species was higher in streams with colder water temperatures. We observed few fish within concealment structure; however, by electrofishing concealment habitat during the day, we captured 10 times more adult trout than we counted immediately beforehand by snorkeling. Adult trout were concealed in cobble-boulder substrate and woody debris during the day.

K. A. Meyer[1]*, J. S. Gregory[2]

[1]Water Resources Team Winema National Forest, Klamath Falls, Oregon, [2]Gregory Aquatics, Mackay, Idaho, USA
* Present address: Idaho Department of Fish and Game, 1414 East Locust Lane, Nampa, ID 83686, USA; e-mail: kmeyer@idfg.state.id.us

Un resumen en español se incluye detrás del texto principal de este artículo.

Introduction

It has been well documented that juvenile trout, including Yellowstone cutthroat trout *Oncorhynchus clarki bouvieri* (Griffith & Smith 1993), brown trout *Salmo trutta* (Griffith & Smith 1993; Heggenes et al. 1993), rainbow trout *O. mykiss* (Campbell & Neuner 1985; Contor & Griffith 1995; Griffith & Smith 1995), and bull trout *Salvelinus confluentus* (Thurow 1997), emerge at night from daytime concealment during winter. Daytime concealment most often occurs in cobble-boulder substrate, woody debris, undercut banks and submerged aquatic macrophytes. It has been suggested that large-bodied adult trout are unable to find suitably sized concealment habitat, especially in the interstitial spaces of cobble-boulder substrate, and instead overwinter above the substrate in deep pools, often forming large aggregations (Bjornn & Reiser 1991; Cunjak 1996).

This assertion, however, is based on few studies that have directly observed diel behavior of adult trout during winter. Campbell & Neuner (1985) found resident adult rainbow trout (≤15 cm in length) concealed in the substrate during the day and resting lethargically on the bottom at night; however, their study streams contained few fish larger than 20 cm. Cunjak & Power (1986) observed adult brown trout and brook trout *Salvelinus fontinalis* aggregating in large main stem pools during the day and speculated that suitably sized concealment habitat was generally absent, but they did not report nighttime observations. Brown trout larger than 25 cm actively aggregated in deep, slow stream areas during the day, whereas smaller fish (<25 cm) sheltered passively in the substrate or in submerged aquatic macrophytes (Heggenes et al. 1993). Thus, assessment of winter diurnal activity of adult trout is lacking, particularly for larger (>20 cm) fish.

Our primary objective was to assess, under a variety of geomorphic stream conditions, whether adult trout exhibited daytime concealment behavior during winter. Concealment behavior in young salmonids appears to begin as water temperatures decline below 7–10°C (Hartman 1963; Chapman & Bjornn 1969; Rimmer et al. 1983; Heggenes et al. 1993; Contor & Griffith 1995) and fish gradually shift to nocturnalism with decreasing temperatures (Fraser et al. 1995). If we found adult trout con-

cealed during the day, our second objective was to assess if a similar shift to nocturnalism occurred in adult trout as water temperatures declined.

Methods

We selected study streams in Idaho (Big Lost River, Parsons Creek) and Oregon (Cherry Creek, Sevenmile Creek) with varying geomorphic and habitat characteristics (Table 1). Underwater observations were made in these streams using a dry suit, mask, snorkel and recording sleeve or bank recorder. One study site of approximately 100 m was established for each stream, and the same site was sampled during each survey. The diver started at the downstream end of the site and proceeded cautiously upstream searching for fish throughout the unit, including the cover components and stream margins. When a fish was encountered, an estimate of total length (TL) to the nearest centimeter was recorded. We regularly calibrated ourselves by aligning the snout and tail with adjacent substrate material and measuring that distance (cf. Cunjak & Power 1986). Our search time was directed at enumeration and not behavioral observations. Because we did not want to disturb fish during the day dives and therefore affect their behavior at night, and because there was a limit to the size of structure we could manipulate (Thurow 1997) to search adult concealment habitat, few rocks or pieces of wood were turned to search for fish. However, efforts were made to rigorously search any concealment habitat where fish could be detected without disturbing the concealment structure, such as woody debris, undercut banks and larger substrate where vision into interstitial chambers was possible. The few fish we did observe when searching concealment structure, we defined as concealed.

Dives typically lasted about 1 hour and were begun between 1200 and 1430 during the day and at least 1 hour after sunset at night. Night dives were aided by the use of a dive-light, with the beam directed to the underside of the water surface to minimize fish disturbance (cf. Contor & Griffith 1995). Underwater visibility exceeded 3 m for each sampling occasion. At each study site water temperatures were recorded hourly through the winter with thermographs, and air and water temperatures were recorded before each dive with a hand-held thermometer. Scale and otolith analysis revealed that fish ≥15 cm TL in Cherry Creek and Sevenmile Creek and Fish ≥20 cm TL in Parsons Creek and Big Lost River were age−2+. The discrepancy was due to colder water temperature, lower productivity and consequently slower growth rates in the Oregon streams than the Idaho streams.

To control for possible variation in nocturnalism through the winter, we stratified our surveys into early, mid- and late winter dives. On the eastern slope of the southern Cascade Range in Oregon, winter typically lasts from mid-November, when water temperatures drop below 7–10°C, to mid-March when rain-on-snow events often lead to an early runoff. Consequently, dives in Oregon were made on 27 November 1996 (early winter), 11 and 12 January 1997 (mid-winter), and 8 March 1997 (late winter). In Idaho, where winter conditions were more prolonged, dives were made on 7 November 1996 (early winter), 3 February 1997 (mid-winter), and 31 March 1997 (late winter).

To compare day and night counts of brook trout and rainbow trout, we used a three-factor repeated measures analysis of variance (ANOVA) blocked by stream with phase (day *vs* night) as a repeated measure and sample period (early, mid- and late winter) as a main factor. To compare patterns of

Table 1. Selected biological and hydrological characteristics of the study streams in Idaho and Oregon at the snorkeling sites

Stream	Latitude/longitude	Elevation (m)	Gradient (%)	Stream order	Rosgen type[a]
Big Lost	43°59′N/113°46′W	1890	0.5	4	C4
Parsons	43°59′N/113°46′W	1890	<0.1	2	C4
Sevenmile	42°42′N/122°04′W	1280	1.0	3	E4
Cherry	42°36′N/122°08′W	1329	3.0	3	B3

Mean wetted width (m)	Mean annual discharge (m³/s)	Mean monthly water temperature (°C)					Available concealment cover[b]
		N	D	J	F	M	
10	9.6	7.5	5.8	5.3	5.6	NA	SWD/LWD
7	0.1	5.5	4.1	3.9	4.3	NA	SWD/UCB
8	0.7	3.7	2.5	2.4	3.2	3.6	LWD/UCB
8	0.7	3.3	NA	1.6	2.1	2.6	CBS

[a] Based on stream type classification in Rosgen (1994).
[b] CBS=cobble-boulder substrate; SMD=small woody debris (<10 cm diameter); LWD=large woody debris (>10 cm diameter); UCB=undercut bank.

diel activity between rainbow trout and brook trout, we first standardized the fish count data by calculating a nocturnal index (Fraser et al. 1995) as follows:

$$100 \times \frac{FC_n}{FC_n + FC_d}$$

where FC_n is the number of fish counted on a given night and FC_d is the equivalent value for that day. We then used the same ANOVA design as above but replaced phase with species. Duncan's multiple range test was used for multiple comparisons when main factors were significant. Water temperatures were warmer in the Idaho streams (4–9°C) than the Oregon streams (1–4°C), thus we compared nocturnal index between streams as an indication of the relationship between nocturnalism and water temperature. Student's t-tests were used to investigate differences in mean size of fish observed during day vs night for each stream. We used SAS (SAS Institute 1987) to perform all analyses.

We assumed that fish we observed at night in excess of those observed during the day were concealed within the study sites and were not moving into the sites between the day and night dives. To test this assumption, we selected a 15-m section of the Big Lost River (within the 100-m study site) that contained most of the woody debris in the study site. On 7 March we snorkeled the 15-m section and performed a two-pass electrofishing removal in the section immediately afterward. Because our intention was only to verify approximate number of adult trout present at the time of snorkeling, and a shallow riffle was present at each end of the 15-m section, block-nets were not used.

Results

In 24 hours of diving, we observed a total of 305 adult trout (78 during day, 227 at night). Water temperatures ranged between 1 and 9°C during our surveys and fluctuated little (never more than 1°C) between day and night dives.

An average of 2.0 times as many adult rainbow trout and 7.5 times as many adult brook trout were counted at night than during the day for all streams combined (Fig. 1); this difference between day and night counts was significant for both rainbow trout ($P=0.009$) and brook trout ($P=0.002$). Only once (Big Lost River, early winter, brook trout) did we count more of one species of trout during the day than at night.

The number of fish counted consistently declined as winter progressed for both species, but the relationship was not significant for rainbow
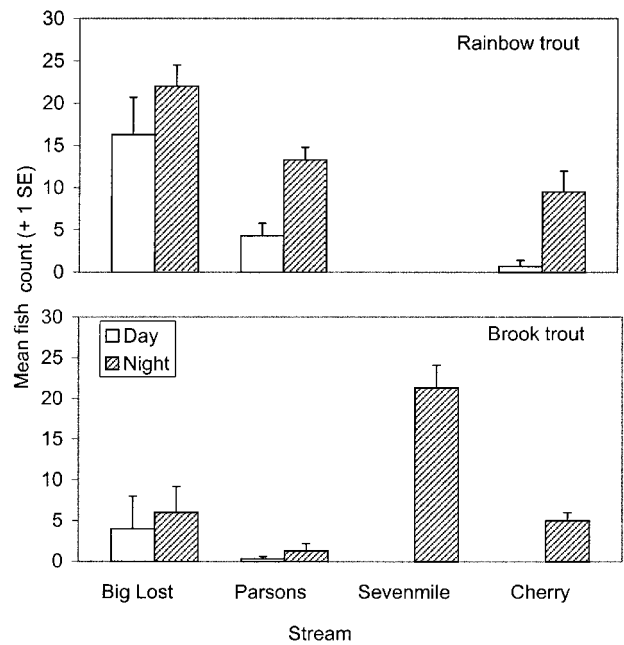

Fig. 1. Mean numbers of adult rainbow trout and brook trout counted during day and night snorkeling surveys in four study streams in Idaho and Oregon
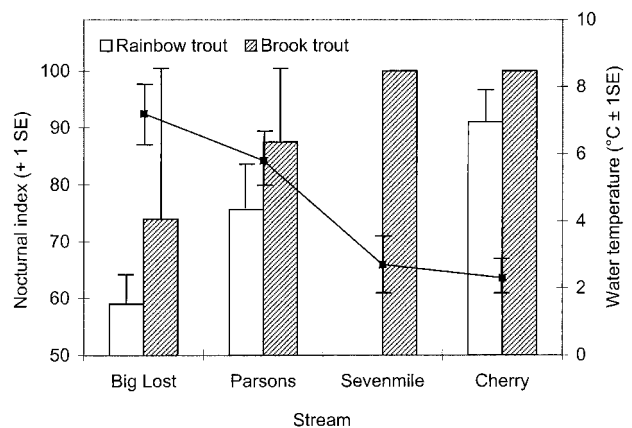

Fig. 2. Mean nocturnal index of rainbow trout and brook trout and average water temperature during snorkeling surveys in four study streams in Idaho and Oregon

trout ($P=0.573$) and only marginally significant for brook trout ($P=0.075$). On average, 25% fewer rainbow trout were observed at night in late winter vs early winter. In contrast, 78% fewer brook trout were observed at night in late winter vs early winter.

The nocturnal index was slightly higher in each stream for brook trout than rainbow trout (Fig. 2), but the difference was not significant ($P=0.504$). Brook trout were exposed during the day at two of the four sites (both Idaho streams) but consistently only in the Big Lost River, whereas rainbow trout were consistently exposed in all locations where
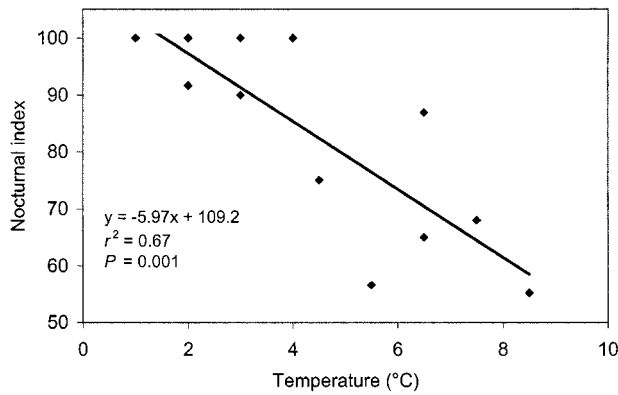
Fig. 3. The relationship between average instantaneous water temperatures (day and night) and nocturnal index of adult trout (rainbow and brook trout combined) during snorkeling surveys in four study streams in Idaho and Oregon

they occurred. The nocturnal index for both species was significantly higher in the streams with colder water temperature ($P=0.034$; Fig. 2) but did not change within each stream over the course of winter ($P=0.446$). Since there was no difference in nocturnalism between species in our ANOVA model, we pooled species to calculate an overall nocturnal index value for each survey and regressed it against average instantaneous water temperature for each paired survey. There was a strong negative relationship between water temperature and overall nocturnal index ($P=0.001$; $r^2=0.670$; $n=12$; Fig. 3).

The estimated size of fish observed did not differ between day and night dives for either species in any of the study streams (Table 2). Though the mean fish length was usually slightly larger during the day than at night, there was never a significant difference for any comparison ($P>0.135$).

In the Big Lost River, trout exposed during the day were always in pools, although most of the trout observed were not in the deepest pool but rather a shallower pool that contained a large, dense complex of small woody debris. At night, some trout were observed in the pools but did not appear to be associated closely with the cover. In Parsons Creek, exposed trout during the day and at night were found in deep pools which contained large, dense patches of small woody debris; however, at night some trout (primarily brook trout) were observed in riffles where the closest cover was undercut banks. In Sevenmile Creek, no fish were ever located during the day, and at night, adult brook trout were almost exclusively observed in holding positions in the large pools adjacent to but well distanced from the complexes of woody material. Exposed fish in Cherry Creek during both day and night were located in pools, behind boulders in mid-channel, or along the stream margins.

Three adult rainbow trout (all $\geq$33 cm) were observed by snorkeling in the abbreviated site in the Big Lost River prior to electrofishing the area. In that same abbreviated site, 29 adult rainbow trout and 1 adult brook trout were captured with the electrofisher in two passes ($N_{hat}=30$, 95% confidence interval 30–32, capture probability 0.882). Most fish were captured from small woody debris in the site. Five of 31 adult trout were $\geq$33 cm and 27 of 31 were $\geq$25 cm. Water temperature during the snorkeling/electrofishing survey was 9°C.

Discussion

Our results indicate that, in winter, many adult trout, at least in our study streams, seek shelter in concealment structure during the day and emerge at night. Previously, this type of behavior has been affirmed only for juvenile salmonids. By concealing during the day, adult trout attain the same ecological benefits that juvenile salmonids gain from concealment, including protection from floods or ice (Hartman 1965), reduced energy expenditure (Heggenes et al. 1993), and avoidance of

Table 2. Sizes of rainbow trout and brook trout observed while day and night snorkeling at each study stream during winter 1996–1997. Means±1 SE are shown

Stream	Day Mean size			Night Mean size		
	n	(cm TL)	Range	n	(cm TL)	Range
			Rainbow trout			
Big Lost	49	31±1	20–41	66	29±1	20–41
Parsons	13	36±1	30–43	41	33±1	20–43
Sevenmile		---NA---			---NA---	
Cherry	3	20±3	17–22	24	18±1	15–22
			Brook trout			
Big Lost	12	28±1	20–36	18	26±1	20–36
Parsons	1	23	---NA---	4	26±2	20–30
Sevenmile		---NA---		64	18±1	15–27
Cherry		---NA---		10	17±1	15–22

predators (Fraser et al. 1993). In a recent study, Valdimarsson & Metcalfe (1998) showed that juvenile Atlantic salmon *Salmo salar* clearly selected refuges that allowed them to hide but offered little shelter from the current, and suggested the primary function of winter nocturnal behavior is to hide from diurnal predators. If hiding from predators is the overriding factor leading adult trout to conceal in winter, it follows that concealment behavior would be reduced when vulnerability is lower, such as under turbid or ice-covered conditions (Young 1995; Gregory & Griffith 1996a, Jakober et al. 1998), neither of which occurred in our streams during our surveys.

Although in winter all juvenile salmonids exhibit nocturnal behavior, our results suggest that in streams and rivers where adult trout do conceal during the day, some adult fish remain diurnally exposed. This may be due to competition for larger spaces, which could result in adult exclusion from daytime concealment, as has been observed with juvenile trout (Gregory & Griffith 1996b). This ultimately could lead to emigration from the area or reduced survival of excluded trout. Such a hypothesis suggests that smaller adults would be excluded from spaces during the day, which is not supported by our finding that the size of rainbow trout and brook trout counted at night did not differ from those counted during the day. Alternatively, adult trout densities are typically lower than juvenile densities, therefore competition may be reduced or absent. Adult trout may be more flexible in their concealment behavior than juvenile trout, shifting between diurnalism and nocturnalism depending on food availability, water temperature, competitive interactions (Brännäs & Alanärä 1997), or other conditions.

The concealment behavior we observed was not limited to the smaller adult trout in the populations. Rainbow trout and brook trout up to 22 cm were concealed during the day in cobble-boulder substrate and up to 43 cm were concealed in small and large woody debris. In contrast to our findings, Heggenes et al. (1993) found adult brown trout up to 25 cm concealed in cobble-boulder substrate and submerged aquatic macrophytes, but larger fish were not concealed. Species differences in habitat suitability (Meyer & Griffith 1997) or the availability of adequately sized concealment chambers (Bustard & Narver 19975; Gregory & Griffith 1996a) may influence the extent of daytime concealment. Our results suggest that, at temperatures ≤9°C, even the larger trout in a given population may become nocturnal if suitably sized concealment habitat is available.

In the Big Lost River, we captured 58% more adult trout from a 15-m section of our 100-m snor-keling site with the electrofisher than we ever counted at night over the entire site, suggesting that all adult trout may not emerge from concealment each night. Griffith & Smith (1993) found that 61–66% of juvenile cutthroat trout and brown trout emerged at night at water temperatures around 7°C, similar to the range of 5–9°C in the Big Lost River. The slower rate of gastric evacuation during winter (36 hours required to evacuate 95% of stomach contents of adult brown trout at 4°C; Elliott 1972) may relax the need to feed each night.

Our results illustrate the need to carefully consider observational methods in future field studies to assess adult trout winter habitat use. Had we only snorkeled during the day, we would have concluded, at least in the Idaho streams, that adult trout overwintered in deep pools above the substrate, as previous daytime snorkeling and radio-telemetry studies have found (Cunjak & Power 1986; Chisholm et al. 1987; Heggenes et al. 1993; Brown & Mackay 1995; Jakober et al. 1998). We believe that searching the substrate and other concealment habitat for sheltered fish, which has been effective for juvenile salmonids (Rimmer et al. 1984; Cunjak 1998; Heggenes et al. 1993; Thurow 1997) and has been recommended as a means of calibrating winter habitat use (Heggenes & Saltveit 1990), will be largely ineffective for adult trout because of the physical size of concealment spaces necessary to hold adult trout and the physical limit to the size of stone or woody debris a snorkeler can overturn. We located only four adult trout during our study that we defined as concealed; two were in Cherry Creek, wedged deep in interstitial chambers between immovable boulders, and two were in Big Lost River, deep in woody debris complexes, all with only a portion of their body visible. Investigations of adult trout winter habitat use may need to use a combination of survey methods, including radio-telemetry, electrofishing, and day/night snorkeling.

Previous studies of juvenile salmonids have found that concealment behavior begins around 7–10°C (Hartman 1963; Chapman & Bjornn 1969; Rimmer et al. 1983; Heggenes et al. 1993; Contor & Griffith 1995); however, in a recent investigation of juvenile Atlantic salmon, Gries et al. (1997) found no threshold to nocturnalism at temperatures up to 23°C. We found adult trout concealed at temperatures ≤9°C but do not know whether a concealment threshold existed. Our temperature *vs* nocturnal index regression suggests that a threshold in our streams may have occurred at 10°C. We suspect that threshold may vary by species and geomorphic characteristics, but this remains to be tested for adult trout. A potentially confounding

factor in the temperature-fish count relationship is that there was no overlap in water temperature between Idaho streams and Oregon streams. Thus, we cannot be certain that the higher fish counts we observed were specifically due to higher temperature and not a difference in fish behavior between the Idaho and Oregon streams. Studies over a wider range of temperatures and seasons (spring and fall) are needed to more fully assess the effect temperature has on adult concealment behavior.

Our study design had some limitations. The small sample size may have led to a failure in finding significant differences in some of the variables in our models that were truly different, but we did not estimate the power $(1-\beta)$ of the tests because retrospective power analysis on observed data and effect size is meaningless (Steidl et al. 1997). Since we did not use block-nets to close our snorkeling sites to fish movement, we cannot be certain that the discrepancy between day and night counts was not the result of fish moving into our study sites after our day dives and before our night dives. However, our snorkeling and electrofishing results suggest this is highly unlikely. We believe, instead, that the fish that were exposed at night in excess of those counted during the day had emerged from daytime concealment.

Our finding that adult trout concealed during the day in winter may have important implications for the management of stream-dwelling salmonids. Considering that trout typically do not reach sizes much larger than those in our streams (except in large rivers and unusually productive streams) and that our observations were made in streams with varying channel characteristics and water tempertures, the concealment behavior we observed by adult trout might be widespread. Research of the magnitude previously devoted to juvenile salmonid winter ecology is needed to assess the extent of adult trout concealment during winter and the effects that stream size and type, fish species and size, water temperature, concealment habitat type and availability, and ice and turbidity conditions have on that concealment and, ultimately, on over-winter survival or carrying capacity of adult trout.

Resumen

1. Se ha realizado poca investigación sobre la ecología invernal de truchas adultas, en particular sobre el comportamiento de escondite. Buceando, comparamos conteos bajo el aqua, de dia y de noche, de adultos de *Oncorhynchus mykiss* y *Salvelinus fontinalis* en cuatro ríos.
2. A temperatura entre 1°C y 9°C, los conteos durante el dia fueron el 44% mientras que el 16% de los conteos por buzeo fueron observados durante la noche para ambas especies. Al avanzar el invierno, los conteos de noche disminuyeron más para *S. fontinalis* que para *O. mykiss* pero esta disminución no fue significativa en ninguna de las dos especies. El nocturnalismo de ambas especies fue mayor en los ríos con temperaturas mas frias.
3. Observamos pocos individuos en estructuras de escondite, sin embargo, durante el dia, capturamos con pesca eléctrica 10 veces más truchas adultas en habitats de escondite que las contadas previamente con buzeo. Las truchas adultas se esconden en sustratos de grava y restos vegetales durante el dia.

References

Bjornn, T.C. & Reiser, D.W. 1991. Habitat requirements. American Fisheries Society Special Publication 19: 83–138.

Brännäs, E. & Alanärä, A. 1997. Is diel dualism in feeding activity influenced by competition between individuals? Canadian Journal of Zoology 75: 661–669.

Brown, R.S. & Mackay, W.C. 1995. Fall and winter movements of and habitat use by cutthrout trout in the Ram River, Alberta. Transactions of the American Fisheries Society 124: 873–885.

Bustard, D.R. & Narver, D.W. 1975. Aspects of the winter ecology of juvenile coho salmon (*Oncorhynchus kisutch*) and steelhead trout (*Salmo gairdneri*). Journal of the Fisheries Research Board of Canada 32: 667–680.

Campbell, R.F. & Neuner, J.H. 1985. Seasonal and diurnal shifts in habitat utilized by resident rainbow trout in western Washington Cascade mountain streams. In: Olson, F.W., White, R.G. & Hamre, R., ed. Symposium on small hydropower and fisheries. Bethesda, MD: American Fisheries Society, pp. 39–48.

Chapman, D.W. & Bjornn, T.C. 1969. Distribution of salmonids in streams, with special reference to food and feeding. In: Northcote, T.G., ed. Symposium on salmon and trout in streams. MacMillan Lectures in Fisheries. University of British Columbia, Vancouver. pp. 153–176.

Chisholm, I.A., Hubert, W.A. & Wesche, T.A. 1987. Winter stream conditions and use of habitat by brook trout in high-elevation Wyoming streams. Transactions of the American Fisheries Society 116: 176–184.

Contor, C.R. & Griffith, J.S. 1995. Nocturnal emergence of juvenile rainbow trout from winter concealment relative to light intensity. Hydrobiologia 299: 178–183.

Cunjak, R.A. 1988. Behaviour and microhabitat of young Atlantic salmon (*Salmo salar*) during winter. Canadian Journal of Fisheries and Aquatic Sciences 45: 2156–2160.

Cunjak, R.A. 1996. Winter habitat of selected stream fishes and potential impacts from land-use activity. Canadian Journal of Fisheries and Aquatic Sciences 53 (Suppl. 1): 267–282.

Cunjak, R.A. & Power, G. 1986. Winter habitat utilization by stream resident brook trout (*Salvelinus fontinalis*) and brown trout (*Salmo trutta*). Canadian Journal of Fisheries and Aquatic Sciences 43: 1970–1981.

Elliott, J.M. 1972. Rates of gastric evacuation in brown trout, *Salmo trutta* L. Freshwater Biology 2: 1–18.

Fraser, N.H.C., Metcalfe, N.B. & Thorpe, J.E. 1993. Temperature-dependent switch between diurnal and nocturnal foraging in salmon. Proceedings of the Royal Society of London B252: 135–139.

Frazer, N.H.C., Heggenes, J., Metcalfe, N.B. & Thorpe, J.E. 1995. Low summer temperatures cause juvenile Atlantic salmon to become nocturnal. Canadian Journal of Zoology 73: 446–451.

Gregory, J.S. & Griffith, J.S. 1996a. Winter concealment by subyearling rainbow trout: space size selection and reduced concealment under surface ice and in turbid water conditions. Canadian Journal of Zoology 74: 451–455.

Gregory, J.S. & Griffith, J.S. 1996b. Aggressive behaviour of underyearling rainbow trout in simulated winter concealment habitat. Journal of Fish Biology 49: 237–245.

Gries, G., Whalen, K.G., Juanes, F. & Parrish, D.L. 1997. Nocturnal activity of juvenile Atlantic salmon (*Salmo salar*) in late summer: evidence of diel activity partitioning. Canadian Journal of Fisheries and Aquatic Sciences 54: 1408–1413.

Griffith, J.S. & Smith, R.W. 1993. Use of winter concealment cover by juvenile cutthroat trout and brown trout in the South Fork of the Snake River, Idaho. North American Journal of Fisheries Management 13: 823–830.

Griffith, J.S. & Smith, R.W. 1995. Failure of submersed macrophytes to provide cover for rainbow trout throughout their first winter in the Henrys Fork of the Snake River, Idaho. North American Journal of Fisheries Management 15: 42–48.

Hartman, G.F. 1963. Observations on behavior of juvenile brown trout in a stream aquarium during winter and spring. Journal of the Fisheries Research Board of Canada 20: 769–787.

Hartman, G.F. 1965. The role of behavior in the ecology and interaction of underyearling coho salmon (*Oncorhynchus kisutch*) and steelhead trout (*Salmo gairdneri*). Journal of Fisheries Research Board of Canada 22: 1035–1081.

Heggenes, J. & Saltveit, S.J. 1990. Seasonal and spatial microhabitat selection and segregation in young Atlantic salmon, *Salmo salar* L., and brown trout, *Salmo trutta* L., in a Norwegian River. Journal of Fish Biology 36: 707–720.

Heggenes, J., Krog, O.M.W., Lindas, O.R., Dokk, J.G. & Bremnes, T. 1993. Homeostatic behavioural responses in a changing environment: brown trout (*Salmo trutta*) become nocturnal during winter. Journal of Animal Ecology 62: 295–308.

Jakober, M.J., McMahon, T.E., Thurow, R.F. & Clancy, C.G. 1998. Role of stream ice on fall and winter movements and habitat use by bull trout and cutthroat trout in Montana headwater streams. Transactions of the American Fisheries Society 127: 223–235.

Meyer, K.A. & Griffith, J.S. 1997. First-winter survival of rainbow trout and brook trout in the Henrys Fork of the Snake River, Idaho. Canadian Journal of Zoology 75: 59–63.

Rimmer, D. M., Paim, U. & Saunders, R.L. 1983. Autumnal habitat shift of juvenile Atlantic salmon (*Salmo salar*) in a small river. Canadian Journal of Fisheries and Aquatic Sciences 40: 671–680.

Rimmer, D.M., Paim, U. & Saunders, R.L. 1984. Changes in the selection of microhabitat by juvenile Atlantic salmon (*Salmo salar*) at the summer-autumn transition in a small river. Canadian Journal of Fisheries and Aquatic Sciences 41: 469–475.

Rosgen, D.L. 1994. A classification of natural rivers. Catena 22: 169–199.

SAS Institute Inc. 1987. SAS user's guide: statistics, version 5 edition. Cary, MC: SAS Institute Inc.

Steidl, R.J., Hayes J.P. & Schauber, E. 1997. Statistical power analysis in wildlife research. Journal of Wildlife Management 61: 270–279.

Thurow, R.F. 1997. Habitat utilization and diel behavior of juvenile bull trout (*Salvelinus confluentus*) at the onset of winter. Ecology of Freshwater Fish 6: 1–7.

Valdimarsson, S.K. & Metcalfe, N.B. 1998. Shelter selection in juvenile Atlantic salmon, or why do salmon seek shelter in winter? Journal of Fish Biology 52: 42–49.

Young, M.K. 1995. Telemetry-determined diurnal positions of brown trout (*Salmo trutta*) in two south-central Wyoming streams. American Midland Naturalist 133: 264–273.

Zar, J.H. 1996. Biostatistical analysis. 3rd edn. Englewood Cliffs, NJ: Prentice Hall.